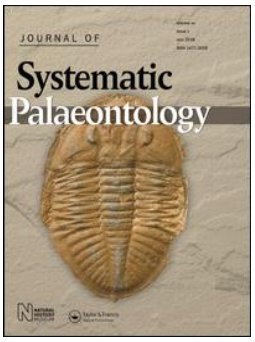

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Making a giant rodent: cranial anatomy and ontogenetic development in the genus *Isostylomys* (Mammalia, Hystricognathi, Dinomyidae)

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South American giant fossil rodents represent a notable example of an extreme evolutionary trend towards size differentiation among caviomorph lineages. Although spectacular, fossil remains of these animals are uncommon and usually highly incomplete. We here describe fully grown adult and juvenile fossil specimens from the rodent family Dinomyidae Alston, 1876, collected from the same location, lithostratigraphical formation and fossiliferous horizon: the coast of the Río de la Plata of southern Uruguay in pelitic sediments assigned to the late Miocene Camacho Formation. The adult remains consist of an almost complete skull with partial jaw and represent the first published description of associated craneo-mandibular remains of a giant rodent within the subfamily Eumegamyinae. The juvenile specimen is the first to be recognized as such for the entire subfamily, and consists of a complete mandible and a right calcaneus. Based on the homologies observed in the configuration of the teeth, the new specimens are assigned to *Isostylomys laurillardi* Kraglievich, 1926, thus demonstrating that the general morphology of the teeth (including the binding pattern) of Eumegamyinae remained unchanged throughout most of their growth. The dental ontogeny of large-sized rodents casts doubt on the validity of the subfamily Gyriabrinae, which may be composed of juveniles of different taxa within other subfamilies of Dinomyidae.

Keywords: Dinomyidae; giant rodent; ontogeny; Miocene; Uruguay

Introduction

During most of the Cenozoic, the continental isolation of South America was one of the main reasons for the limited faunal exchange with other regions of the world. This isolation resulted in reduced and discontinuous migrations, and the promotion of local diversification in many endemic and 'new-arriving' lineages (Simpson 1940; Pascual *et al.* 1996). One of these groups includes the endemic mid-sized rodents of the infraorder Caviomorpha (Wood 1955; Huchon & Douzery 2001; Poux *et al.* 2006; Sallam *et al.* 2009, Patton *et al.* 2015), which represent an important part of the current diversity of rodents on the subcontinent (Woods 1982; Woods & Kilpatrick 2005; Solari *et al.* 2012). The first undisputed caviomorph record of the group comes from the middle Eocene deposits at Contamana, in the Peruvian Amazonia, from which tiny primitive forms closely related to some African Oligocene hystricognaths have been identified (Antoine *et al*. 2012). The group experienced an *in situ* early radiation, achieving a multiplicity of ecomorphotypes whose most remarkable aspects include the independent appearance (during the Miocene) of large-sized to gigantic forms in several lineages. One of these is the Family Dinomyidae, Alston 1876, which includes the largest rodent ever recorded, currently placed in the superfamily Chinchilloidea (Rinderknecht & Blanco 2008; Rinderknecht *et al*. 2011).

Although the fossil record of Dinomyidae is diverse and extensive (see Rinderknecht *et al*. 2011), it currently includes only the pacarana (*Dinomys branickii*), a cursorial and enigmatic Amazonian caviomorph considered to be among the largest living rodents (Collins & Eisenberg 1972; White & Alberico 1992; Nasif & Abdala 2015). Fossil Dinomyidae are putatively known from as early as the middle Miocene (Friasian: South American Land Mammal Age (SALMA)), showing a clear increase in abundance and diversity during the middle-to-early late Miocene (Laventan to Huayquerian SALMAs). Although the first described fossils of the family date back to the late 19th century (Ameghino 1883, 1885, 1886, 1889, 1891a, b; Burmeister 1885), the phylogeny of Dinomyidae has never been addressed or tested using a modern cladistics approach (but see Nasif 2009 for an unpublished phylogeny of the group). A brief review of the history and

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Figure 1. Unedited original portrait of the great Argentine palaeontologist Lucas Kraglievich (1886–1932) who, among many contributions to the field of South American vertebrate palaeontology, established the general criteria for the current systematic arrangement of Dinomyidae.

scientific knowledge of fossil dinomyds was provided by Rinderknecht & Blanco (2015).

Almost all current knowledge of Dinomyidae is based on the remarkable work done by the Argentine palaeontologist Lucas Kraglievich (Fig. 1), whose main contributions on the topic were reported at the beginning of the twentieth century. Kraglievich's investigations, published as detailed notes, communications and extended monographs, some posthumous, gave rise to the present systematic arrangement of the entire family, addressing diverse aspects of the anatomy and taxonomy of the Dinomyidae (Kraglievich 1926, 1930, 1932, 1934). His review of the group included almost all known specimens deposited in the collections of national history museums in both Argentina and Uruguay, leading to the description of new species, genera and subfamilies, and the fundamentals of systematic stability for more than the 60 fossil species currently recognized (Kraglievich 1926, 1930; Fernández de Álvarez 1947; Bondesio 1978; Mones 1986). Following this historical arrangement, later complemented and corrected by Fields (1957) and Pascual (1967), the family was subdivided into four or five subfamilies: Potamarchinae (including the oldest known representatives of the family, which extends from the middle Miocene to the late Pliocene); Gyriabrinae (late Miocene to late Pliocene, medium-sized forms); Dinomyinae (which includes only the extant pacarana, *Dinomys branickii*); Eumegamyinae (late Miocene to late Pliocene forms, including the largest representatives of the family); and Tetrastylinae (late Miocene to Pliocene, also medium-sized tetralophodont forms), which many authors consider to be a subgroup of the Eumegamyinae or Dinomyinae (Fields 1957). Although this systematic scheme has been sustained over the years with minimal changes, it is important to note that current knowledge of the anatomy of these animals is clearly insufficient. This is due to the lack of associated cranial and postcranial remains, with almost all of the named species being based on fragmentary remains, mostly consisting of isolated teeth and/or small fragments of skulls or mandibles (Mones 1986). Such an incomplete record limits any possibility of developing a comprehensive comparative analysis of the different lineages within Dinomyidae, hindering the understanding of the phyletic trajectory experienced by this notable group of rodents during their evolution.

Fortunately, in recent years, our research team has made significant progress on fossil dinomids, including the naming of a new genus and recognition of the potential of the auditive region for taxonomic characterization (Rinderknecht *et al*. 2011). In addition, we described *Josephoartigasia monesi* Rinderknecht & Blanco, 2008, the largest rodent ever recorded, providing a detailed palaeobiological investigation (Rinderknecht & Blanco 2008; Blanco *et al*. 2011; Cox *et al.* 2015). In this new contribution, we report the discovery of a new giant, nearly complete skull and mandible of a full-growth adult of the Miocene genus *Isostylomys* Kraglievich, 1926. This is the first description of an almost complete skull of this genus and its associated mandible. We also present the first known remains of an undisputable juvenile Eumegamyinae, composed of an exceptionally well-preserved mandible with complete dentition and the associated right calcaneum. This specimen is also assigned to the genus *Isostylomys*. All of the fossils were exhumed at the same locality and stratigraphical position at the base of the local exposures of the late Miocene Camacho Formation, and they represent some of the best-preserved remains of giant dinomids known to date. The new materials allow us to perform a detailed investigation of the dental morphology and its variation during growth in this genus. The different hypotheses proposed since the nineteenth century related to the dental ontogenetic development in these rodents are tested for the first time. Based on our results, we also review the taxonomic status of all of the species described within the genus *Isostylomys*, proposing a new taxonomic arrangement for the genus and extending our comments in relation to the systematic validity of one of the most enigmatic subfamilies – Gyriabrinae – within the dinomids.

Materials and methods

As a comparative framework oriented toward analysing the ontogenetic development of the Eumegamyinae, we studied specimens in different stages of growth from the genus *Dinomys* (the only living Dinomyidae), along with the largest living rodent, the capybara (*Hydrochoerus hydrochaeris*). The criteria selected for determining the age range/stage of the samples in the case of *Hydrochoerus hydrochaeris* were taken from Ojasti (1971), who related degree of cranial sutures with age. In *Dinomys*, ontogenetic stages were addressed through the direct observation of collection specimens, examination of high-quality photographs taken from materials deposited in scientific collections from Peru, Colombia, Argentina, England, France and Uruguay, and recently published descriptions (Nasif & Abdala 2015). The upper teeth are designated using capital letters (P4, M1–M3), and the lower teeth designated with lowercase letters (p4, m1–m3).

The traditional ontogenetic stages of eutherian mammals (prenatal, infant, juvenile, adult and senile) were deduced from the fusion of the epiphyses, sutures in the skeleton, the tooth eruption sequence and the degree of wear (Sánchez-Villagra 2010; Nasif & Abdala 2015). Because most fossil dinomids are only known from isolated teeth or fragmentary dentitions, any proposed model devoted to determining the age of these rodents must rely on the characteristics observed in the teeth. Unfortunately, these kinds of models are somewhat limited for extant caviomorph rodents with ever-growing hypselodont teeth, as many of them are born with permanent dentition that undergoes little change throughout their life. For these reasons, this study considers three stages of ontogenetic development: prenatal, juvenile, and full-growth adult stages.

All of the new fossil specimens reported here were collected by Luis R. Castiglioni and are housed in the palaeontological collection of the Museo Nacional de Historia Natural in Montevideo, Uruguay (**MNHN**). The examined specimens that were used in the comparisons and their institutional abbreviations are listed in the online Supplementary material.

Institutional abbreviations

Fossil and extant specimens utilized in this analysis belong to the following institutions. **NHMUK**: Natural History Museum, London, UK; **MACN**: Colección paleontológica del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MACN-A**: Colección Ameghino del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MACN-M**: Colección Mastozoológica del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MNHN**: Museo Nacional de Historia Natural, Montevideo, Uruguay; **MLP**: Museo de La Plata, La Plata, Argentina; **UDCA-UIFS:** Unidad de Investigación en Fauna Silvestre de la Universidad de Ciencias Aplicadas y Ambientales, Bogotá, Colombia; **UNMSM-MUSM**: Colección de Mastozooología del Museo de Historia Natural de la Universidad Nacional de San Marcos, Lima, Peru.

Geological setting

The fossil-bearing strata are located in south-western Uruguay (San José Department; 34° 34′ S, 56° 58′ W) in exposures located on the coastal cliffs and littoral platform of the Río de La Plata. Here, the lithostratigraphical units recognized from base to top are the Camacho (late Miocene), Raigón (Pliocene and Pleistocene) and Libertad (Pleistocene) formations (Bossi & Navarro 1991; Tófalo *et al*. 2009). The first two units yield many vertebrate fossils, including a variety of dinomids currently under study.

The Camacho Formation is the Uruguayan representation of an extended, late Miocene, eustatic event regionally known as the ‘Paranean transgression’ or ‘Paranean Sea’. In the San José department, this includes facies related to the regressive phase, characterized as estuarine and/or paralic environments. Terrestrial and freshwater vertebrates in association with marine invertebrates and ichnofossils compose the fossil assemblage of the unit (Ubilla *et al*. 1990; Perea *et al*. 1996; Sprechmann *et al*. 2000; Verde 2002; Perea 2005). Sediments of the Camacho Formation are formed by greenish-grey, friable and medium compressed pelite that becomes greenish-brownish towards the top of the formation. The mammalian fossil assemblage includes marsupial carnivores, xenarthrans, hystricognath rodents, notoungulates, litopterns and cetaceans, showing affinities with the late Miocene Chasicoan and Huayquerian Ages/Stages of Argentina, especially with the stage informally known as the ‘Mesopotamiense’ (formerly considered as a Huayquerian age local fossil fauna) of Entre Ríos Province (Perea *et al*. 1994, 2013; Perea 2005; Cione and Tonni 2005; Brandoni 2013). ^{40}Sr/^{39}Sr dated levels of the Paraná Formation and its southern correlative, the Puerto Madryn Formation, give a late Miocene 9.5–10 Ma (Tortonian) age for the top of the ‘Paranean Sea’ in Argentina. Recently, Bostelmann & Rinderknecht (2010) reported the presence of *Hemihegetotherium achataleptum*, a common early late Miocene biostratigraphical indicator from these beds. In addition, Rinderknecht *et al*. (2011) described a new dinomid, *Arazamys castiglionii*, from outcrops of the San José Department.

The overlying Raigón Formation is considered fluvio-deltaic (Bossi 1966) or fluvial (Tófalo *et al*. 2009), with swamp-related channel-filled and floodplain facies. Its lithology includes green-clayed, fine- and medium-grained white sands and conglomerate levels (Bossi 1966). It is considered to be of Pliocene age, but the occurrence of certain Ensenadan age mammals, such as *Catonyx tarijensis*, suggests that its deposition ended during the early Pleistocene (McDonald & Perea 2002). Fossil mammals, while less abundant than in the Camacho Formation, include ground sloths, cingulates, notoungulates, and Hydrochoerinae and Eumegamyinae rodents, particularly the largest known taxa (Francis & Mones 1966; Mones 1989; Rinderknecht & Blanco 2008). Large phorusrhacid (Tambussi *et al*. 1999) and anhingids (Rinderknecht & Noriega 2002) are notable fossil birds exhumed in this formation.

Systematic palaeontology

Order **Rodentia** Bowdich, 1821
Infraorder **Hystricognathi** Tullberg, 1899
Superfamily **Chinchilloidea** Kraglievich, 1940a
Family **Dinomyidae** Alston, 1876
Subfamily **Eumegamyinae** Kraglievich, 1932
Genus ***Isostylomys*** Kraglievich, 1926
Isostylomys laurillardi (Ameghino, 1883)
(Figs 2–8)

Holotype. MACN 5823, anterior portion of left mandible.

Synonyms. *Isostylomys ameghinoi* Kraglievich, 1932; *Isostylomys laevis* Rusconi, 1945; *Isostylomys intermedius* Mones & Castiglioni, 1979; and *Isostylomys magnus* Mones & Castiglioni, 1979.

Age. Late Miocene, Tortonian Age, ?Chasicoan/ ?Huayquerian SALMA.

Material. MNHN 2187, skull and mandible: an almost complete skull of an adult specimen, slightly distorted during diagenesis, lacking the posterior part of the braincase. Two dentaries of the same specimen (Figs 2–5). MNHN 2687, two dentaries and right calcaneum of a juvenile specimen (Figs 4–8).

Description. Skull and upper teeth (MNHN 2187). Gigantic size (Table 1); larger than any other known rodent except for *Josephoartigasia monesi*, which is slightly larger and more robust. As in all Eumegamyinae, the nasals are wide, with laterally expanded frontals. The lacrimal apophysis is robust, and the parasagital crest is strong and posteriorly convergent. Slender zygomatic arches compared with other caviomorph rodents like Ctenomyidae, Chinchillidae and Dasiproctidae, with the anteorbitarian bar posteriorly located beginning at M3 transverse plane. Both characters are also shared with *J. monesi*, the only one Eumegamyinae in which the zygomatic arch has been preserved. The foramen opticum is not visible laterally due to a marked posterior displacement, differing from all remaining caviomorph rodents, in which it is located anteriorly. This particular feature is also observed in both *J. monesi* and *Eumegamys paranensis*, leading us to considerer it as a new diagnostic character for the subfamily Eumegamyinae.

The incisors are well developed (Fig. 3), with tiny longitudinal ridges in the enamel face, which are difficult to appreciate at first glance. The upper cheek teeth present a typical prismatic shape, formed by lophs of dentine surrounded by a thin enamel lamina, wider on the anterior face of the tooth. A thin layer of cementum separates these lophs from each other, with the anterior lophs being more laterally expanded than the posterior ones (Fig. 4).

The P4 is pentalophodont, with the first three lophs free and constituting separate units, and the two posterior lophs joined by the lingual face (a diagnostic character of the genus *Isostylomys*). Both M2 and M3 are pentalophodont, with the first two lophs free and the three posterior lophs being joined at the lingual side. In the right M3, the fifth loph is composed of three small cylindrical enamel columns, more or less joined to each other. These characteristics were first considered by earlier scholars to represent a pathological condition or an atavism that naturally tended to be reduced during the ontogenetic process (or evolution) of the different species (Kraglievich 1940c). Another cylindrical, small, enamel column is present in the labial border of the third and fourth lophs on both M3.

Mandible and lower teeth (MNHN 2187). The two dentaries are preserved and fused with each other, lacking the ascending ramus and the angular process. The symphysis reaches the anterior border of m1. The notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle (= deep masseter) is located in the external wall, under the transverse plane of m1 and m2. The left p4–m3 series is fully preserved and displays a similar, but inverted structure in relation to the arrangement and morphology of the upper teeth lophs, with the posterior lophs being more laterally developed than the anterior ones (Fig. 5). It is also apparent that the enamelled face of the upper lophs is wider on its anterior face, whereas in the lower teeth, the posterior face is the widest. In the upper teeth, the posterior lophs are lingually joined, but in the lower teeth, this condition is inverted, with the anterior lophs labially joined. Finally, in the upper teeth, the anterior face of each molar is concave, while it is convex in the lower teeth. Consequently, due to this symmetrical inversion, each lower tooth is similar to the respective upper tooth on the opposite side. Thus, the left p4 could be attached to the alveolus of the right P4 without causing any differences. This situation can occur in all of the teeth of the Eumegamyinae except in the last upper molar because M3 usually yields one more loph than m3. Additionally, M3 can present reduced enamel accessory columns in the posterior portion of the tooth. These

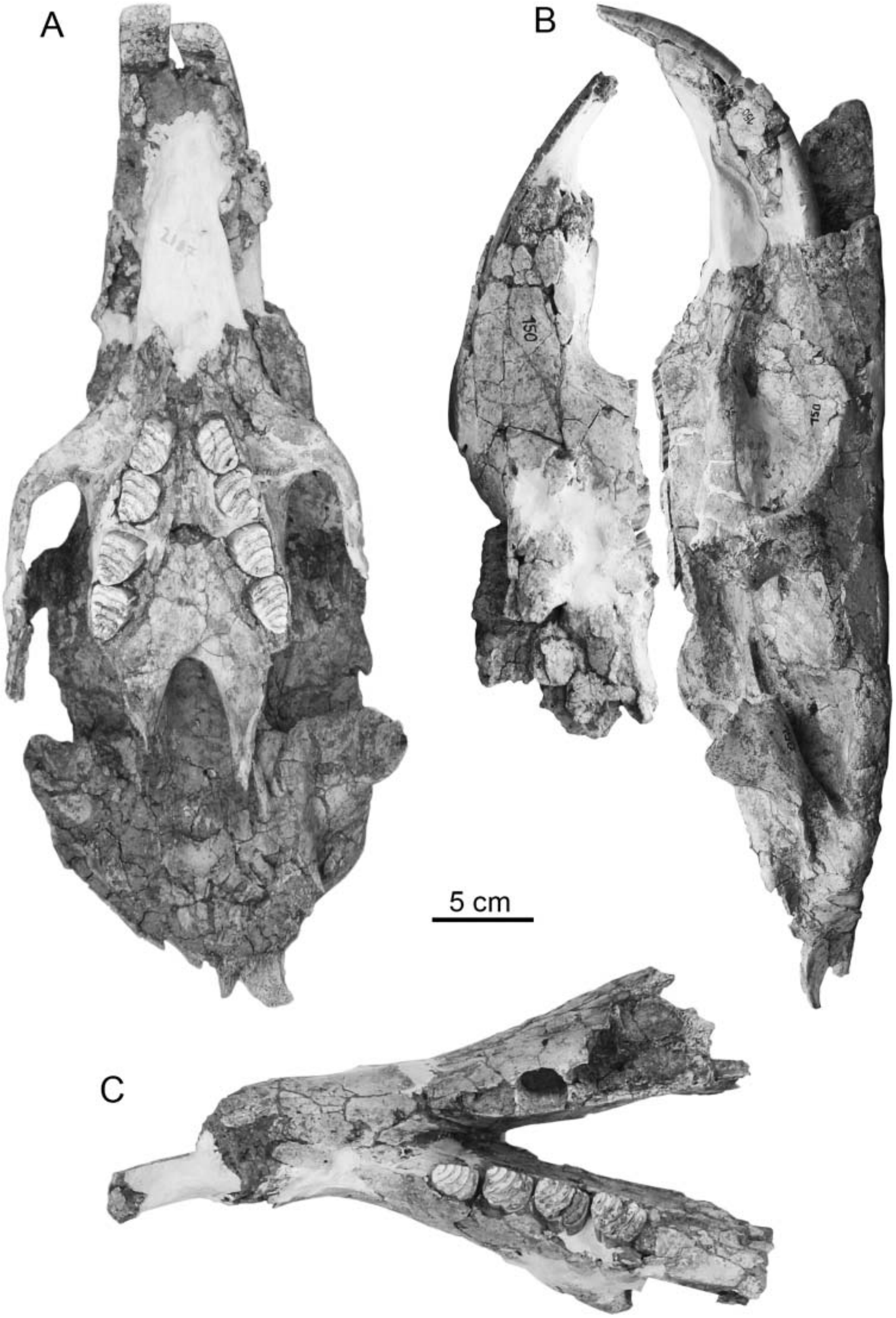

Figure 2. *Isostylomys laurillardi*, MNHN 2187. **A**, skull in ventral view; **B**, skull and mandible in left lateral view; **C**, mandible in occlusal view.

structures do not occur in m3, at least in the adult specimens. The m1 and m2 are pentalophodont, with the three first lophs labially joined and the two posterior lophs free. The m3 is also pentalophodont with the first three lophs labially joined and the two posterior lophs free. Both lower incisors were preserved, being similar to the upper ones. The conformation of each lower tooth, with five lophs, and the p4 with the two anterior lophs labially jointed, is a diagnostic feature of Isostylomys.

Juvenile mandible (MNHN 2687). The mandible includes both dentaries, which are nearly complete, exhibiting excellent preservation (Fig. 6). This material probably represents the most complete mandible ever recorded in a

Table 1. Dental measurements (in mm) of *Isostylomys laurillardi* (MNHN 2187).

	Mesiodistal length	Buccolingual width
Right P4	25.5	18.1
Right M1	25.2	20.0
Right M2	25.3	19.8
Right M3	25.3	19.0
Left P4	26.1	19.7
Left M1	25.1	21.3
Left M2	25.0	21.2
Left M3	27.6	20.2
Right I	—	24.8
Left I	—	24.3
Left p4	21.6	15.5
Left m1	24.1	21.3
Left m2	27.0	20.4
Left m3	26.7	22.0
Left i	—	23.3
Right i	25.1	23.2

fossil dinomyid. The most remarkable feature is its small size (half the size of the MNHN-2187 mandible, see Table 2) and the porosity of the bone surface, a condition commonly observed in juvenile rodents and mammals in general (see Ray 1964; Vucetich *et al.* 2005). The morphology of the mandible follows the overall pattern observed in Eumegamyinae, with: (1) a poorly developed horizontal crest; (2) the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle located under m1 and m2; (3) a low mandibular condyle; and (4) a barely visible reduced coronoid process, forming a small uneven surface on the posterolabial side at the m3 level.

The incisors are roughly similar to those of MNHN 2187. Except for the difference in size, each tooth of the p4–m3 series is equal to those described for the genus *Isostylomys*. This similarity extends to the pattern of fusion among the lophs and the proportions of the teeth. Both *rami* are unfused. An X-ray image allowed the observation that all teeth are permanent, with well-defined parallel margins (Fig. 7).

Juvenile calcaneum (MNHN 2687). The right calcaneum was collected in association with the juvenile mandible. Despite being almost complete (it lacks only the articular surface of the cuboid), it is not easy to describe, due to its low degree of ossification. Because of this, the articular surfaces are somewhat diffuse (Fig. 8). The bone is robust and massive, very similar to that observed in Dinomys, and presents an unfused tuber calcis separated from the rest of the bone, indicating a typical juvenile condition.

Figure 3. *Isostylomys laurillardi*, MNHN 2187. Right lower incisor.

Discussion

Dental development in the Eumegamyinae

The possibility for dinomids to change their dental morphology during ontogenetic development has been a topic of discussion for almost a century. The first researcher to address this issue in detail was Lucas Kraglievich, who warned about the likelihood that juveniles of the family

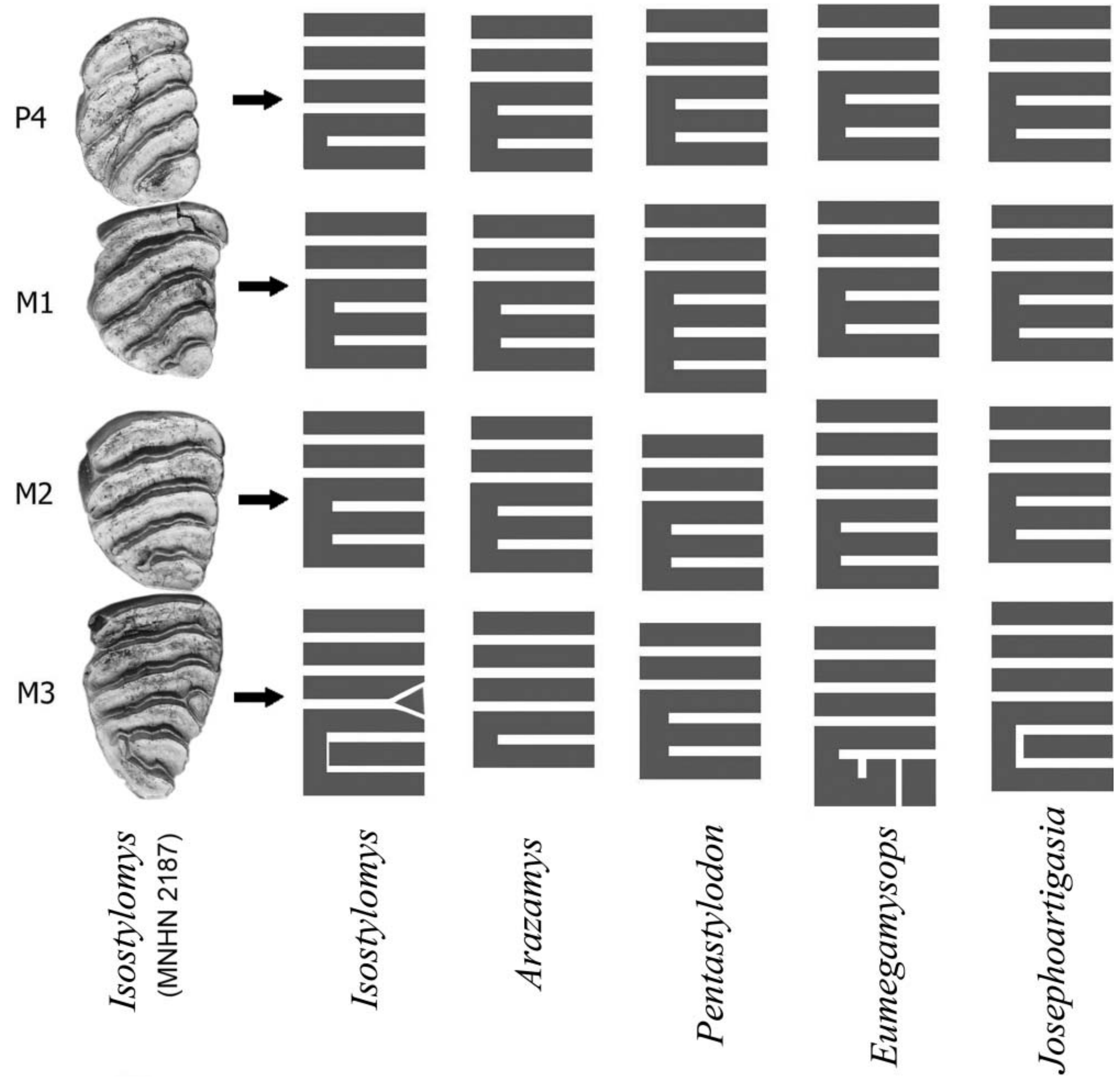

Figure 4. Left P4–M3 of *Isostylomys laurillardi*, MNHN 2187, in occlusal view, and schematics (not to scale) of upper cheek-tooth in different eumegamine genera.

'Eumegamyidae' (= Dinomyidae) might display a greater number of lophs in their teeth compared with full-growth adults (Kraglievich 1926). This statement was supported by observations of the juvenile molars of the genus *Phoberomys* (included within the dinomids at that time and currently located within the family Neoepiblemidae), which shows 'temporary enamel folds'. Wear of these temporary folds can lead to changes in the binding pattern between two lophs along the tooth, or even complete merger, forming just one loph. Thus, the occlusal surface of a tooth could present more lophs than the base, making reasonable to expect that putative juveniles could present teeth with more lophs than the adults.

Later, Kraglievich (1930) interpreted ontogenetic variations in the enamel folds of the teeth of Gyriabrinae but considered these changes to continue in the adults, presuming that members of this subfamily would experience changes in the structure of the teeth during much of their lifespan. Despite these observations, Kraglievich also indicated that Eumegamyinae would acquire the final conformation of the teeth very early in their ontogenetic development.

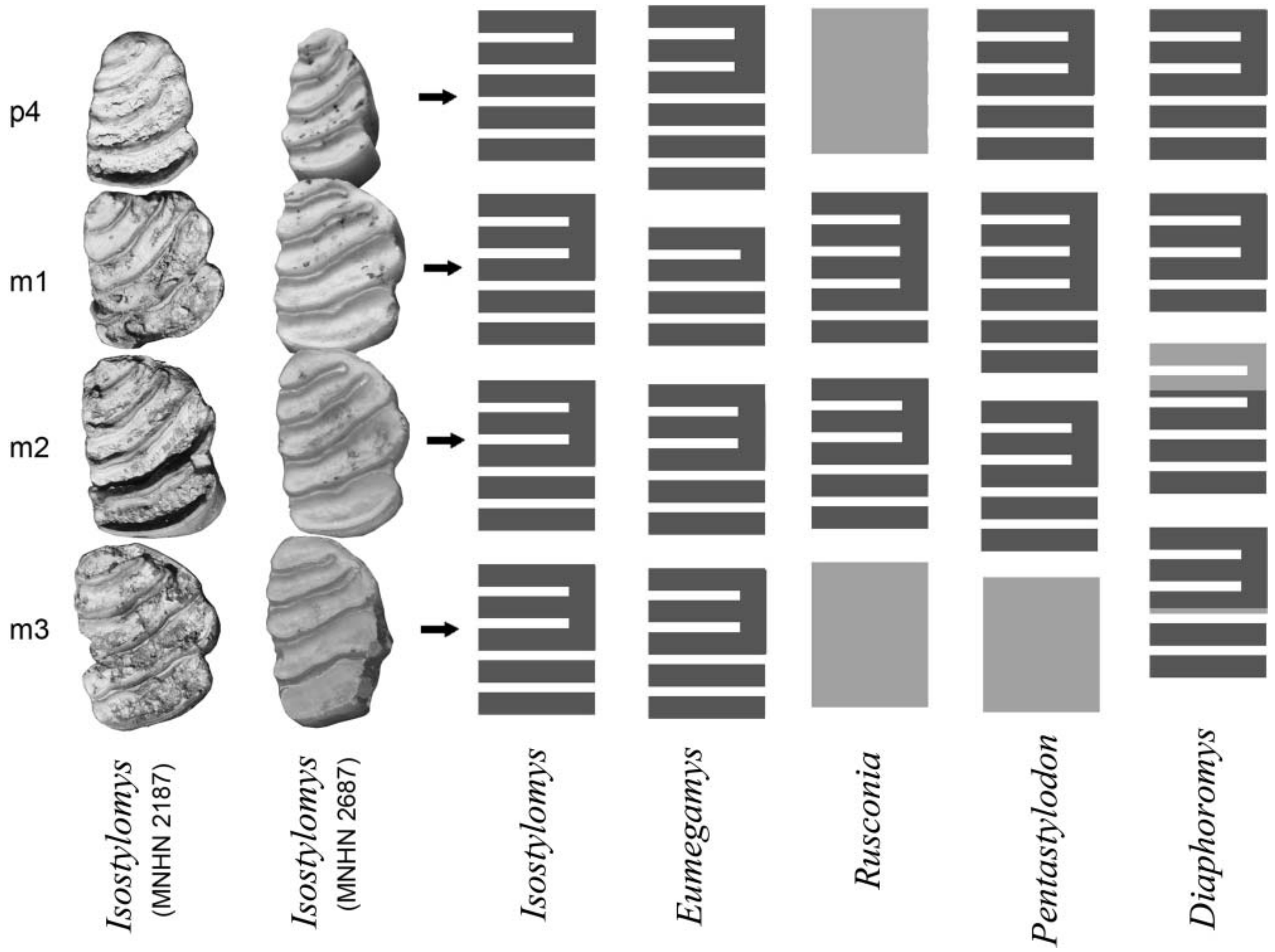

Figure 5. Right p4–m3 of *Isostylomys laurillardi*, MNHN 2187, reversed side, and MNHN 2687) in occlusal view, and schematics (not to scale) of upper cheek-tooth in different eumegamines.

The next palaeontologist who considered ontogenetic variation of the teeth of dinomids was Robert W. Fields, who produced an important series of observations on fossil Eumegamyinae and Potamarchinae in his work on the medium Miocene rodents from La Venta, Colombia (Fields 1957). In his opinion, Kraglievich's hypothesis was correct in relation to the greater number of lophs that are observable in juveniles compared to adults. Fields also suggested that each individual could experience differential degrees of wear, depending on the tooth position. This situation may arise because newly born dinomids retain a deciduous tooth (fourth premolar) and an un-erupted last molar. Hence, the wear on M1/m1 and M2/m2 begins before the wear on P4/p4 and M3/m3, making it reasonable to find juveniles that show the final conformation of M1/m1 and M2/m2, but still have a fourth premolar and third molar with accessory lophs. To support this explanation, Fields considered the holotype of *Eumegamys paranensis* (MLP 15-245), a partial small dentary that presents a p4 composed of six lophs, and interpreted it as a juvenile whose final dental conformation (relative to the number of lophs in the p4) had not yet been acquired. Based on these observations, Fields proposed formal synonymy of the vast majority of the taxa within the subfamily Eumegamyinae, including the genus *Isostylomys*, which he considered a junior synonym of *Eumegamys.*

Fields' proposals have not been taken into account by most subsequent researchers (see Mones & Castiglioni 1979; Mones 1981, 1986; Rinderknecht *et al*. 2011). However, MacPhee (2011) considered them valid based on subsuming *Eumegamysops* (one of the best-known dinomids) within *Eumegamys*. Our investigations show that Fields' proposal has inconsistencies related to the timing of eruption, number of lophs, and degree of wearing on the teeth, making it unreliable, at least for hypselodont Dinomyidae.

According to Fields, the p4 of the type material of *Eumegamys paranensis* shows six lophs (and not five, which is usual in most known Eumegamyinae) because it is expected to have belonged to a 'juvenile' individual in

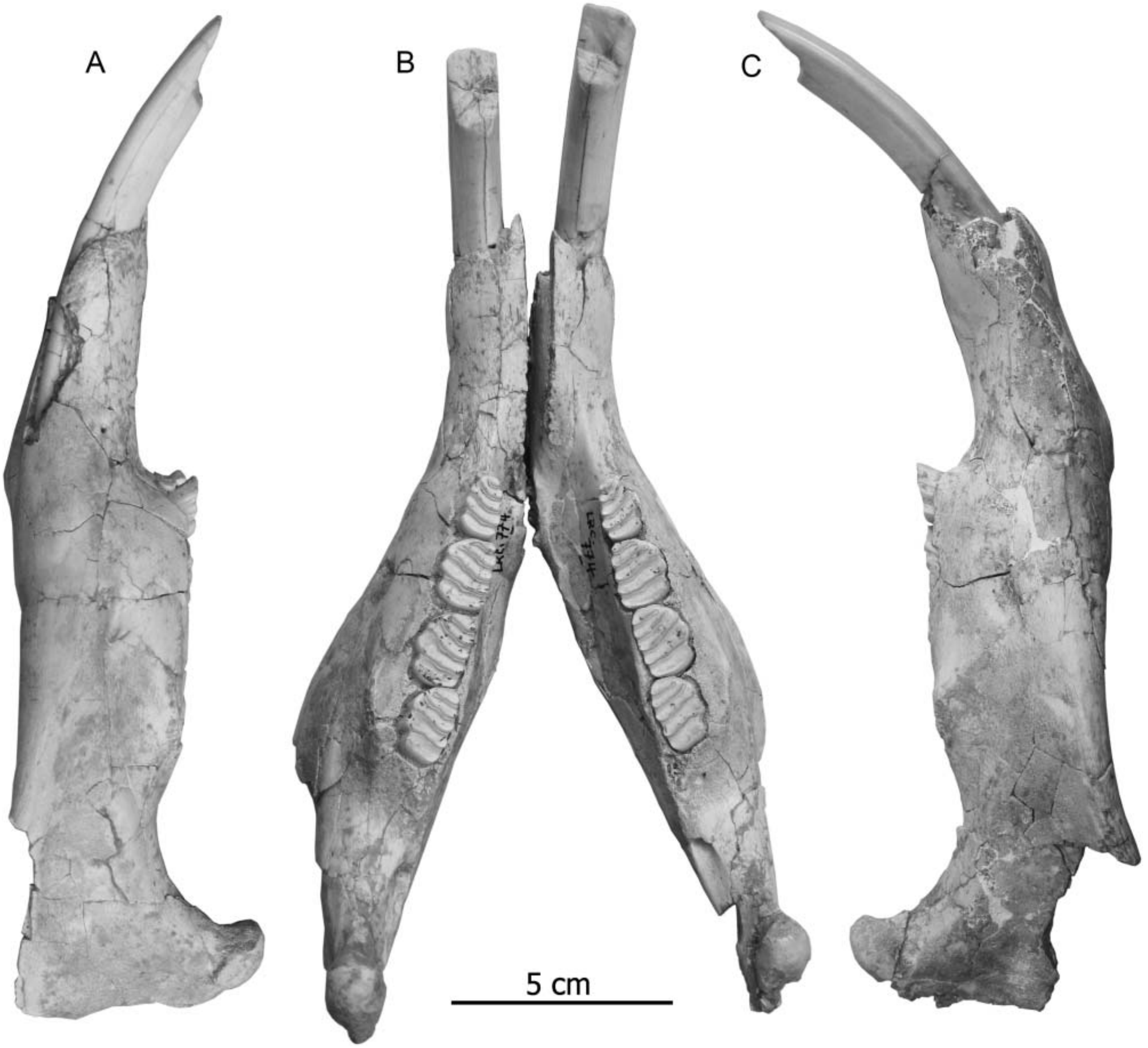

Figure 6. *Isostylomys laurillardi*, MNHN 2687. **A**, left dentary in lateral view; **B**, mandible in occlusal view; **C**, right dentary in lateral view.

Table 2. Dental measurements (in mm) of *Isostylomys laurillardi* (MNHN 2687).

	Mesiodistal length	Buccolingual width
Right p4	12.4	8.4
Right m1	15.0	12.0
Right m2	16.0	12.3
Right m3	15.9	10.9
Left p4	12.9	8.3
Left m1	14.5	11.4
Left m2	16.5	11.9
Left m3	15.7	10.8
Right i	10.4	11.8
Left i	10.2	11.5

which this tooth had recently erupted, without experiencing the loss of lophs that supposedly occurs during ontogenetic development. However, the m1 of the jaw has four lophs, and not five, as observed in all other eumegamines. Following Fields, if *Eumegamys paranensis* represents a juvenile individual, the mandible could not have presented an m1 with fewer lophs than the adult specimens assigned, for example, to *Isostylomys*. In summary, if the jaw of *Eumegamys paranensis* bears a p4 composed of six lophs due to the existence of an accessory loph, which Fields proposed as a characteristic of a less-worn tooth, it would also have been unlikely to lose one loph in m1, bearing in mind the pentalophodont condition observed in almost all eumegamyines.

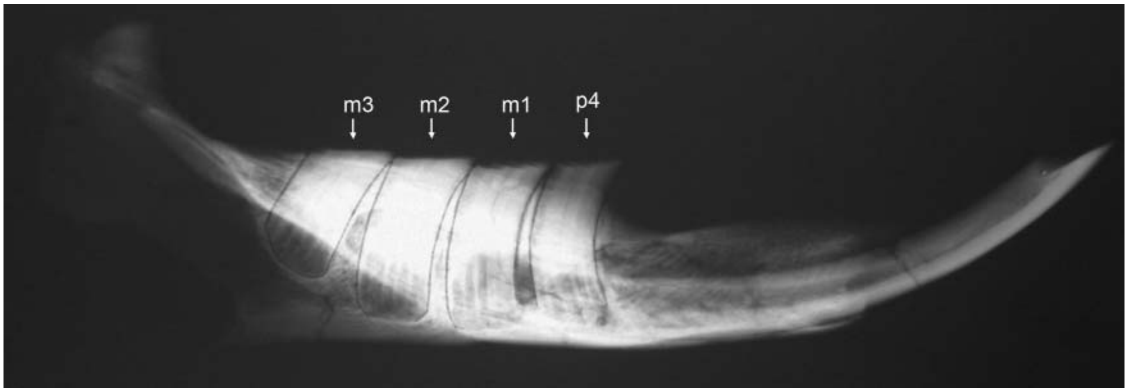

Figure 7. *Isostylomys laurillardi*, MNHN 2687. X-ray image of right dentary in lateral view.

It is important to note that some *Isostylomys* jaws described over a century ago are smaller than the type jaw of *Eumegamys paranensis* but show the same dental topology as the fully growth adults of the genus, with a p4 and m1 composed of five lophs. We consider that all of these contradictions challenge the proposed synonymy suggested by Fields. Moreover, recent studies on the anatomy of the auditory region in Eumegamyinae and its correlation with the dental morphology (Rinderknecht *et al*. 2011) also indicate a lack of support for this taxonomic scheme.

However, Fields' misconception does not mean that there may be named Eumegamyinae that are actually juvenile stages of other taxa. We have shown that, even accepting the thesis that juveniles of a referred taxon exhibited more lophs than the adults, *Eumegamys* cannot be a juvenile of *Isostylomys*. Our findings also call into question the notion that juveniles of Eumegamyinae have more lophs than the adults because the *Isostylomys* juvenile described here clearly shows the dental conformation of a full-growth adult. This implies that in the Eumegamyinae, the full dental conformation would be acquired very early in ontogenetic development, at least when great size differences exists between adults and juveniles.

There have been no previous reports of fossil Eumegamyinae as small as MNHN 2687, with the sole exception of MACN-A 5879, an isolated tooth assigned to *Isostylomys ameghinoi*, which shows a similar size compared with MNHN 2687. It is reasonable to consider that all of the specimens reported as Eumegamyinae in the scientific literature might then correspond to development stages within a single phyletic line. We indeed consider that all of the described specimens that currently constitute the subfamily Eumegamyinae may represent individuals that had attained the definitive condition of the tooth morphology at the time of their death, independent of their ontogenetic status (as adults or juveniles).

While there are few studies on the ontogenetic development of *Dinomys*, some published works (Ray 1964; Mones 1997; Nasif & Abdala, 2015) and specimens held in different collections allow us to speculate on the potential ontogenetic development of the fossil species, using it as an 'actualistic' model.

One remarkable feature of the mandibular ontogeny of the pacarana is related to the final configuration of the teeth, which are acquired when juveniles are almost the size of full-growth adults. When the jaws of a juvenile *Dinomys* reach 65–70% of their final size, m3 has not yet erupted, and dp4 is still present. MNHN 2187 is identical to MNHN 2687 but twice the size. Based on this size relationship, we can assume that *Dinomys* does not serve as a good analogue for the giant fossil forms. Another important feature to highlight is that *Dinomys* specimens do not experience loss of lophs during dental growth, with the sole exception of the m1, which may suffer, in some adult individuals, the incomplete fusion of the anteriormost two lophs. In newborn animals with recently erupted teeth, several unconnected enamel columns with rounded cusps make the occlusal surface. These structures merged to form the lophs, driven by progressive wear during the early ontogeny (Mones 1997; Nasif & Abdala 2015).

In contrast, the ontogenetic development of the capybara has been extensively studied (Kraglievich 1940b; Ojasti 1971; Vucetich *et al*. 2005; Aeschbach *et al*. 2016). Because it is the largest living rodent, we assume that dental growth in the capybara during its ontogeny could be of potential use as a model for comparisons with the Eumegamyinae. In the capybara, when the juveniles exhibit jaws with 60% of the size of the adult jaw, they acquire the final configuration of the dental topology (see Ray 1964). The maximum age reported for a capybara is approximately 12 years, and although the cranial configuration (and the rest of the skeleton) shows ontogenetic changes until approximately five years (Ojasti 1971), the jaw attains the general morphology of the adults (with the exception of the size and degree of ossification) between 17 and 19 months.

This situation implies that in the capybara, the general mandibular morphology forms very early in ontogenetic development, while a large difference in size remains between juveniles and adults. The same situation could

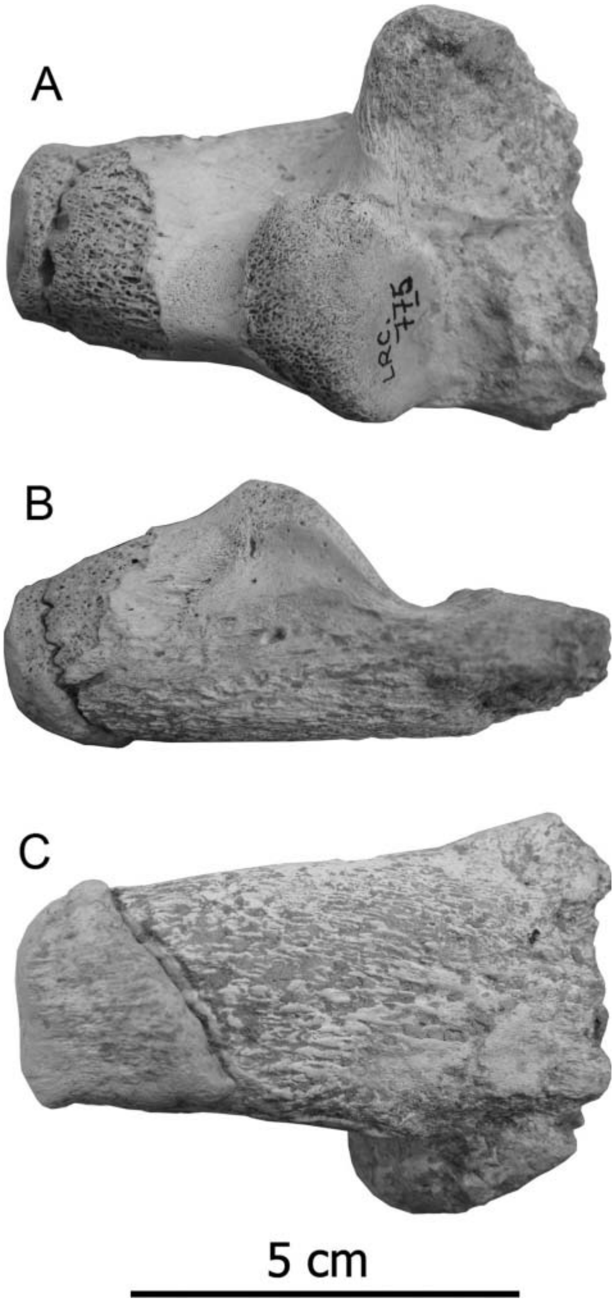

Figure 8. *Isostylomys laurillardi*, MNHN 2687. Right calcaneum in A, dorsal, B, external, and C, plantar views.

have occurred in Eumegamyinae according to the characteristics observed in specimens MNHN 2687 and MNHN 2187.

Large body size may have been the main factor responsible for the mandibular growth of eumegamines during ontogeny, becoming more similar to *Hydrochoerus* than to *Dinomys*. We are aware that our assumptions are based on only two fossil specimens, and the discovery of more material will therefore be necessary to test these conclusions with greater confidence. Changes in mandibular proportions during ontogeny have been recorded in *Dinomys*, including alterations in the vertical orientation of the symphyseal region or the development of the angular process (Nasif & Abdala 2015). Nevertheless, the fragmentary nature of the Eumegamyinae fossil record makes it difficult to assess such changes in these fossil forms. We must also consider that size differences might exist within Eumegamyinae because of intraspecific variation and/or sexual dimorphism. The existence of significant differences in the adult sizes of large fossil rodents has been suggested previously (Biknevicius *et al*. 2003; Horovitz *et al.* 2006). Nevertheless, the differences between the two specimens of *Isostylomys* described herein (Table 3) surpass all intraspecific variations and/or sexual dimorphisms in size reported for any other rodent species (see MacPhee 1984; Patton *et al.* 2015). It is important to note the fact that even though an individual can acquire the final tooth shape very early in ontogenetic development, this does not mean that intraspecific variation may not exist in relation to the morphology of the teeth within Eumegamyinae. In fact, important intraspecific variations have been corroborated in adults *Dinomys*, especially with regard to degree of fusion in enamel columns and binding lophs patterns (see Nasif & Abdala 2015). These variations can be seen in the P4, M3 and p4.

Table 3. Height of mandibles (in mm) in juvenile and adult specimens of *Isostylomys laurillardi* (MNHN 2187 and MNHN 2687).

Mandible height	MNHN 2187	MNHN 2687
At level of left p4	87	35.24
At level of left m3	62.9	36.8
At level of right p4	85	35.8
At level of right m3	—	37.8

On the species of the genus *Isostylomys*

The first report of the genus *Isostylomys* was based on a fragment of a jaw from Argentina, assigned by Ameghino (1883) to the species *Megamys laurillardi* (MACN-A 5823). Later, Kraglievich (1926) demonstrated that this genus (originally proposed by the naturalist Charles Léopold Laurillard) was erected on remains belonging to an ungulate mammal, and transferred all the fossil rodent material included by Ameghino in *Megamys* to the new genera *Eumegamys* (naming the species *Eumegamys paranensis* and *E. scalabrinianus*) and *Isostylomys* (recognizing one species, *Isostylomys laurillardi*).

Posteriorly, the species *Isotylomys ameghinoi* Kraglievich, 1932, *Isostylomys laevis* Rusconi, 1945, *Isostylomys intermedius* Mones & Castiglioni, 1979 and *Isostylomys magnus* Mones & Castiglioni, 1979 were proposed, all differentiated based exclusively on size.

Mones & Castiglioni (1979) did not recognize substantial differences between *Isostylomys laevis*, *I. ameghinoi* and *I. laurillardi* and therefore considered the first two species as synonyms of *I. laurillardi*. In their opinion, the genus *Isostylomys* was only composed of the species *I. laurillardi* (the smallest species), *I. intermedius* (named for an isolated tooth collected in Uruguay), and *I. magnus* (the largest species, also erected from isolated dental remains).

A particular case arises from the review of historical repositories. In the palaeontological collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires, one small isolated tooth (MACN 4708) is labelled as a new species of *Isostylomys*, although it was never formally published. This small ever-growing tooth is 1 cm long in the anteroposterior dimension and 3 cm tall. Five nearly horizontally projecting lophs form the occlusal surface of the tooth. The three anterior lophs are joined on the lingual side, and the labial sides remain free achieving the general pattern of *Isostylomys*. The first loph is the smallest and rounded, with a fragmented tip. The second loph is intermediate in size, with the labial side wider than the lingual side and both the first and third lophs being joined with narrow constrictions. The remaining two distal lophs are free, with the third being the most extended in the buccolingual (transverse) dimension. As is common in all eumegamines, all of the lophs are separated from each other by a thin layer of cement. There is no published record mentioning, or even announcing the existence of this proposed new species. Nevertheless, the adjoining hand-written label reads "(Type) 4708. *Isostylomys minimus* n.sp. Krag. (M) sup. der." and as such, it is recognized as a type specimen in the catalogue of the museum collection. The geographical origin of the specimen is the Barrancas del Río Paraná, Entre Ríos Province, Argentina, the same general locality for the majority of known records of eumegamyines (Nasif *et al.* 2013). Given the isolated nature of this tooth, almost certainly a juvenile, and the absence of adequate diagnostic characteristics, we consider it more appropriate to refer to this material as an undetermined Eumegamyinae.

Size differences, which are the only characteristic used to differentiate all the species within *Isostylomys*, are clearly inadequate for use as a specific characteristic, as *I. laurillardi* and *I. intermedius* are potentially juvenile specimens. Surprisingly, this consideration was never taken into account by previous researchers, probably because of a general belief that juvenile eumegamines should show differences in the number of lophs in relation to the adults. Our research demonstrates that the definitive lower dental morphology of the members of this subfamily is acquired early during ontogenetic development, and that *I. laurillardi*, which shows a remarkable difference in size from *I. magnus*, could indeed represent the same species.

Unfortunately, the meagre state of preservation of the type material of *Isostylomys laurillardi* (MACN-A 5823) does not allow an undisputed assignment regarding its adult or juvenile condition. However, a topotype of this species (MLP-15-247, consisting of a right mandibular ramus) shows the characteristic degree of ossification that suggests a juvenile condition similar to the one observed for MNHN 2687. Considering all this evidence, we propose the formal synonymy of the three present species within the genus – *I. laurillardi*, *I. intermedius* and *I. magnus* – which should be recognized uniquely as *Isostylomys laurillardi*.

On the validity of the subfamily Gyriabrinae

Previously, we concluded that all of the species described in the literature as eumegamines are individuals that had already attain the final configuration of their teeth. This does not mean that eumegamines whose dental configurations were not finally established at the time of death do not exist in the fossil record. However, if these fossils exist, they must have been erroneously placed in other groups.

The subfamily Gyriabrinae (Kraglievich 1930) has a biochron extending from the late Miocene to the late Pliocene and includes nine species assigned to the genera *Gyriabrus* and *Pseudosigmomys*. Gyriabrines are small-sized dinomids recorded in Argentina, Uruguay, Peru and possibly Colombia and Brazil (Paula Couto 1983; Mones 1986; Sant'Anna-Filho 1994). They have been classically considered as basal representatives in the transition to fully hypselodont forms. The subfamily includes all dinomids that have transitional enamel folds in the teeth as adults. According to Kraglievich (1930), these folds are evident on the occlusal surface but tend to disappear with wear, causing changes in the binding pattern and progressively reducing the number of lophs (Fig. 9). Young gyriabrines would therefore exhibit teeth with more lophs than the

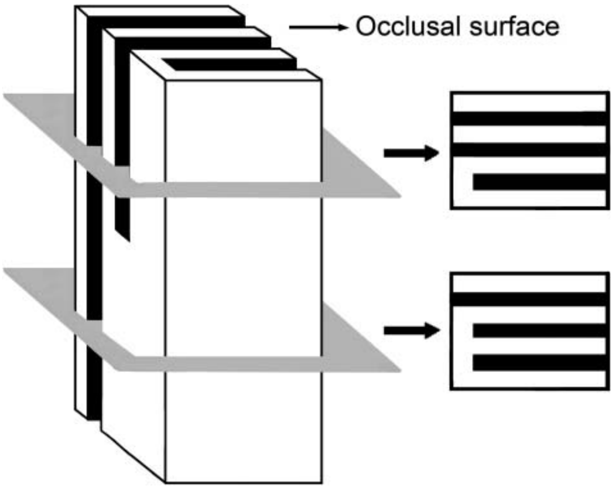

Figure 9. Schematic drawing of a Gyriabrinae tooth.

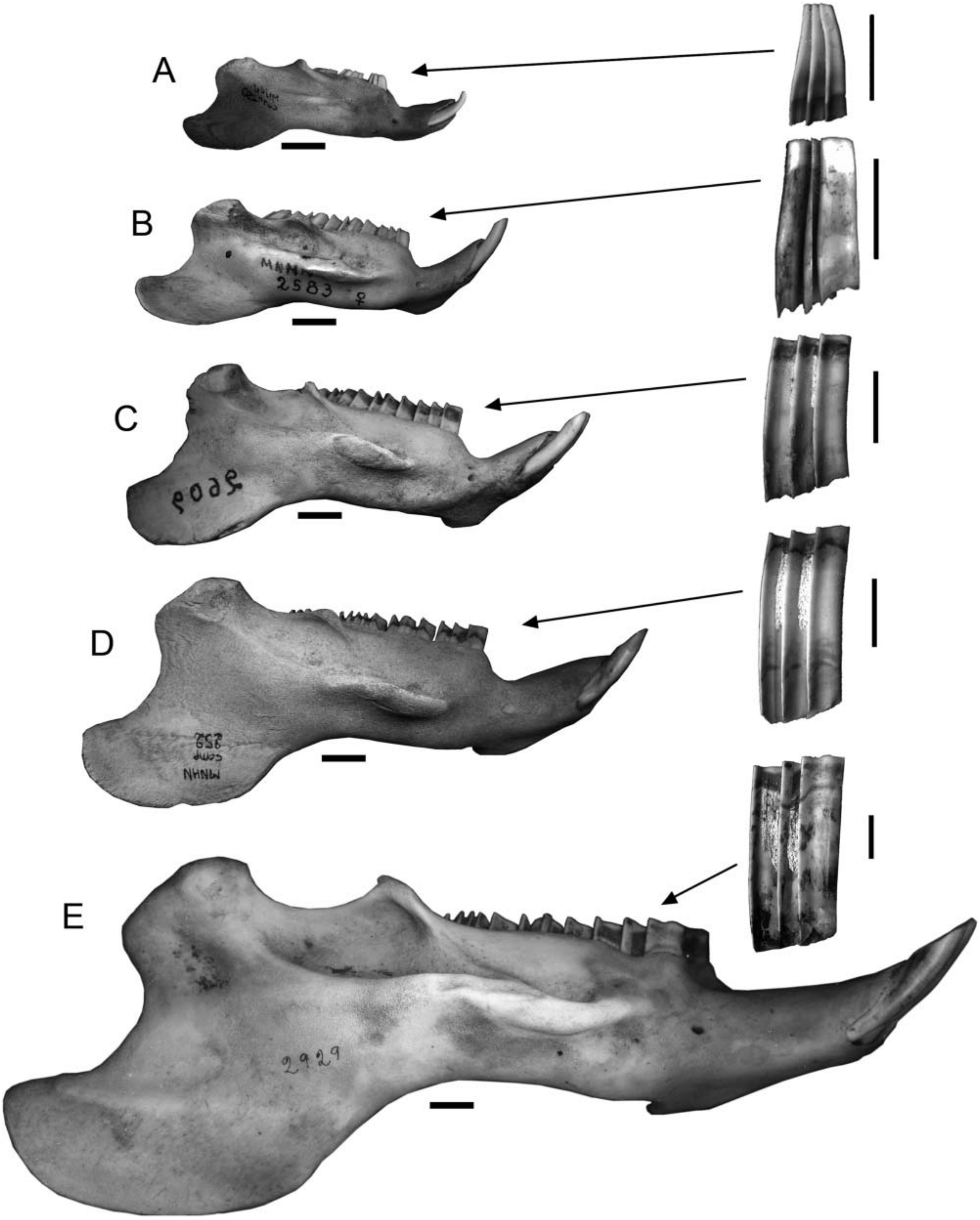

Figure 10. Right dentary of *Hydrochoerus hydrochaeris* and right p4 in different ontogenetic stages. **A**, MNHN 250, unborn specimen; **B**, MNHN 2583, nine days to seven months; **C**, MNHN 2609 (reversed side), seven to 10 months; **D**, MNHN 252 (reversed side), 18–21 months; **E**, MNHN 2929, specimen over four years old. Scale bars = 10 mm.

adults, whereas senile individuals would exhibit teeth with fewer lophs than the adults. The gyriabrines described thus far show a binding pattern of the lophs on the occlusal surface that is different from the one preserved at the base, but changes in the number of lophs along the tooth have only been recorded in the type material of *Gyriabrus glutinatus* (MACN-A 5881), consisting of a badly preserved isolated molar. Therefore, the claim that the gyriabrines showed a reduced number of lophs with wear is hypothetical for almost all known fossils assigned to the group.

It is within Gyriabrinae that the greatest morphological diversity of dental patterns in Dinomyidae is concentrated, although all of the fossils included in this subfamily are dramatically fragmentary and composed of only isolated teeth, fragments of jaws, and palates.

The fact that the morphology of a hypselodont tooth changed with wear (and therefore with the age of the animal) could indicate that the tooth belonged to a juvenile specimen. Kraglievich was aware of this observation, but in his opinion, the Gyriabrinae were not juveniles, but full-growth adults that exhibited morphological changes in their teeth throughout their life (the presumed main diagnostic feature of the subfamily). The argument put forth by the Argentine palaeontologist was that all Gyriabrinae teeth present an occlusal surface with the same width as the base, lacking the common 'cone' shape expected for juvenile hypselodont teeth (Kraglievich 1930, p. 222).

However, in accordance with Vucetich *et al.* (2005), our research shows that there are rodents that may exhibit parallel-sided teeth without completing their ontogenetic development. This occurs in the capybara, which bears cone-shaped teeth only during the early stages of its growth. A few months after birth, capybaras lose their cone-shaped teeth despite being much smaller than the adults (Fig. 10), while retaining morphological differences in the occlusal pattern of some of the teeth (Vucetich *et al*. 2005). This means that the largest living rodent passes through four stages during its ontogenetic dental development: a first stage with cone-shaped teeth, where the binding pattern of the lophs is not definitive; a second stage with parallel edges of the teeth, where the binding pattern of the lophs are still not definitive (the stage that potentially represents the Gyriabrinae); a third stage in which the teeth of the juveniles are indistinguishable from those of the adults except for their size (the stage of specimen MNHN 2687); and finally, the full-growth adult stage (Fig. 9). Following this, all the available evidence allows for an alternative hypothesis to Kraglievich's proposal that the Gyriabrinae represent adult animals. The question then arises of whether the subfamily in question can be maintained, as the only diagnostic feature proposed is precisely the existence of dental changes throughout much of the lifespan of the individuals. On the other hand, our observation shows that the vast majority of Gyriabrinae are almost indistinguishable (except for their small size and the presence of enamel folds) from other taxa allocated to different subfamilies of Dinomyidae. Gyriabrines would therefore not be juvenile specimens from a monophyletic group, as some taxa from this subfamily, such as *Gyriabrus teisseirei* (MNHN 1342), are remarkably similar to some members of Tetrastylinae (and, thus, *G. teisseirei* is likely a young specimen of a large form, such as *Telicomys*). Other taxa show great similarities to members of the Eumegamyinae (such as *Gyriabrus holmbergi* MACN-A 3956; MACN-A 5879). It seems that the false premise that juvenile rodents cannot have parallel-sided teeth led to inclusion of all the specimens showing this growing stage into an artificial group: the subfamily Gyriabrinae (see Fig. 11). The respective synonyms that might arise from our proposal are a subject that cannot be

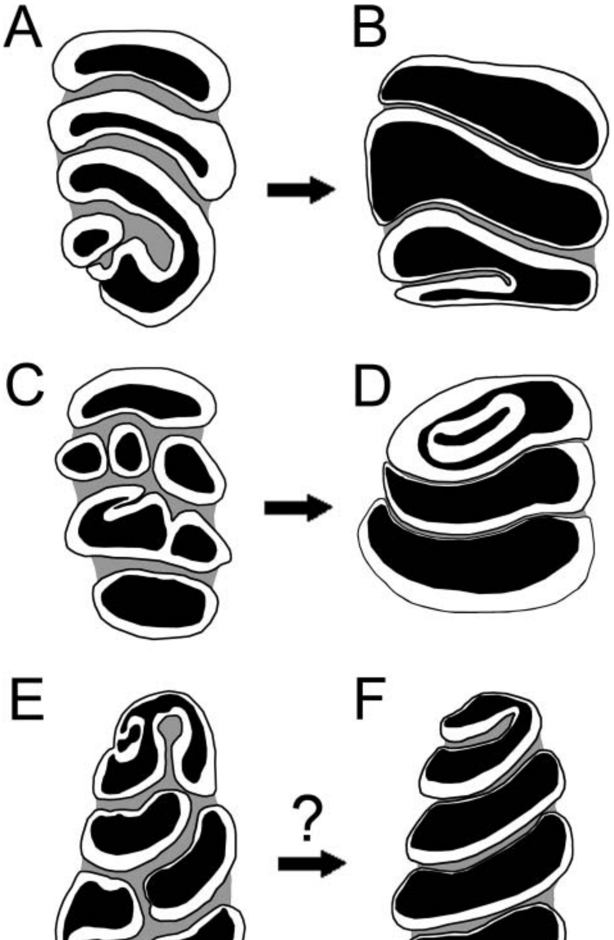

Figure 11. Occlusal view of Dinomyidae adult and juvenile teeth (not to scale). **A,** NHMUK 12.1.15.14, *Dinomys branickii* juvenile, right M1; **B,** NHMUK 3796, *Dinomys branickii* adult, right M1; **C,** MACN 12962, *Dinomys branickii* juvenile, left m1; **D,** NHMUK 34.9.10.191, *Dinomys branickii* adult, left m1; **E,** MACN 3954, *Gyriabrus holmbergi*, right p4; **F,** MNHN 2687, *Isostylomys laurillardi*, right p4.

securely resolved at present, due to the limited and fragmentary nature of the known fossil material. Hence, it is not possible to take the degree of ossification of the mandibular remains, for example, as a criterion for verifying the juvenile condition of fossils included in Gyriabrinae. Therefore, the known fossil remains assigned to this subfamily cannot be categorically placed as juveniles of already known taxa in other subfamilies, but our investigations do allow questioning of the validity of the subfamily Gyriabrinae as a natural group, pending new findings that could corroborate or refute this hypothesis.

Conclusions

A new fossil of an adult specimen of *Isostylomys laurillardi* (MNHN 2187) is described here, which represents the first known associated craneo-mandibular remains of a representative of the subfamily Eumegamyinae. We also report a juvenile specimen (MNHN 2687) of this species from the same location and lithostratigraphical unit. The two fossils exhibit a homologous morphology, where the sole difference is that MNHN 2187 is twice the size of MNHN 2687.

Based on comparisons between the Uruguayan remains and a detailed review involving specimens from different collections, we conclude that Eumegamyinae acquire the final form of their teeth very early during their ontogenetic development. The small size of the mandible of the juvenile specimen and the large size of the adult (only slightly smaller than that of *Josephoartigasia monesi*, the largest known rodent), suggests that all of the remains described thus far as Eumegamyinae correspond to individuals that had already attained the final configuration of the teeth. These findings allow the dismissal of earlier proposals of synonymy within Eumegamyinae (i.e. Fields 1957), based solely on presumed ontogenetic variation involving the number of lophs within the teeth. These findings do not exclude the possibility that intraspecific variation may exist (i.e. polymorphism) related to the binding pattern of lophs in the teeth of the Eumegamyinae.

Based on our observations, we propose formal synonymy of the three known species of the genus *Isostylomys* into just one species, *Isostylomys laurillardi*.

The analysis of the ontogenetic development of *Dinomys* and especially the capybara casts doubt on the validity of the subfamily Gyriabrinae, whose members could represent juvenile specimens of different taxa within the subfamilies Tetrastylinae, Eumegamyinae and Potamarchinae.

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Supplemental material

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